

Influence of climate change factors on carbon dynamics in northern forested peatlands

C. C. Trettin¹, R. Laiho², K. Minkkinen², and J. Laine³

¹Center for Forested Wetlands Research, USDA - Forest Service, Charleston, South Carolina 29414, USA;

²Department of Forest Ecology, University of Helsinki, Helsinki, Finland; ³Parkano Research Station, Finnish Forest Research Institute, Parkano, Finland. Received 20 May 2004, accepted 30 September 2005.

Trettin, C. C., Laiho, R., Minkkinen, K. and Laine, J. 2006. **Influence of climate change factors on carbon dynamics in northern forested peatlands.** *Can. J. Soil Sci.* **86**: 269–280. Peatlands are carbon-accumulating wetland ecosystems, developed through an imbalance among organic matter production and decomposition processes. Soil saturation is the principal cause of anoxic conditions that constrain organic matter decay. Accordingly, changes in the hydrologic regime will affect the carbon (C) dynamics in forested peatlands. Our objective is to review ecological studies and experiments on managed peatlands that provide a basis for assessing the effects of an altered hydrology on C dynamics. We conclude that climate change influences will be mediated primarily through the hydrologic cycle. A lower water table resulting from altered precipitation patterns and increased atmospheric temperature may be expected to decrease soil CH₄ and increase CO₂ emissions from the peat surface. Correspondingly, the C balance in forested peatlands is also sensitive to management and restoration prescriptions. Increases in soil CO₂ efflux do not necessarily equate with net losses from the soil C pool. While the fundamentals of the C balance in peatlands are well-established, the combined affects of global change stressors and management practices are best considered using process-based biogeochemical models. Long-term studies are needed both for validation and to provide a framework for longitudinal assessments of the peatland C cycle.

Key words: Peatland, carbon cycle, methane, forest, wetland.

Trettin, C. C., Laiho, R., Minkkinen, K. et Laine, J. 2006. **Influence des paramètres du changement climatique sur la dynamique du carbone dans les tourbières boisées nordiques.** *Can. J. Soil Sci.* **86**: 269–280. Les tourbières sont un écosystème de type « terre humide » qui emmagasine le carbone. Elles dérivent du déséquilibre entre la production et la décomposition de la matière organique. La saturation du sol est la cause principale d'une anoxie qui entrave la désagrégation des substances organiques. Une modification de l'hydrologie affectera donc la dynamique du carbone dans les tourbières boisées. Les auteurs voulaient passer en revue les études écologiques et les expériences effectuées sur les tourbières en exploitation en vue de mieux évaluer les répercussions d'une modification de l'hydrologie sur la dynamique du carbone. De leur étude, ils concluent que les répercussions du changement climatique se feront principalement sentir à travers le cycle de l'eau. Un abaissement de la nappe phréatique attribuable à une modification du régime pluvial et à l'élévation de la température atmosphérique pourrait réduire la concentration de CH₄ dans le sol et accroître les émissions de CO₂ à la surface de la tourbière. Par voie de conséquence, le bilan du carbone des tourbières boisées est lui aussi sensible aux méthodes d'exploitation et de restauration. Une hausse de l'efflux de CO₂ du sol ne signifie pas obligatoirement une diminution nette des réserves de carbone du sol. Même si on connaît bien les principes fondamentaux du bilan du carbone dans les tourbières, il vaut mieux examiner les effets combinés des facteurs de stress du changement planétaire et des pratiques d'exploitation avec un modèle reposant sur les processus biogéochimiques. Il faudrait entreprendre des études de longue haleine pour valider ces modèles et mettre en place un système qui autorisera une évaluation longitudinale du cycle du carbone dans les tourbières.

Mots clés: Tourbières, cycle du carbone, méthane, forêt, terres humides

Peatlands are carbon (C)-accumulating wetland ecosystems that are sustained by an imbalance between organic matter production and decomposition processes. The net effect over the millennia has been the accumulation of soil organic matter, such that peatlands now contain a disproportionate share of the terrestrial C pool (Maltby and Immirzi 1993). These peatlands comprise approximately 3% of the terrestrial surface of the earth and contain approximately 357 Pg of C, which is 24% of the terrestrial soil C pool (Eswaran et al. 1993; Batjes 1996). Accordingly, the effects of global climate change on C dynamics in peatlands have important ramifications for the stability and long-term storage of the accumulated organic matter, greenhouse gas emissions (e.g., CO₂, CH₄, and N₂O emissions), as well as

many associated ecosystem functions and services that are provided by peatlands (Gitay et al. 2001).

Climate change is most commonly considered as elevated atmospheric CO₂ and the associated increase in mean annual temperature, but there are also other factors, including altered precipitation regimes, atmospheric nitrogen deposition, and elevated ozone concentrations. In peatlands, where the hydrologic regime is the principal factor controlling ecosystem processes, any changes in water balance should be expected to have far-reaching effects on biogeochemical cycles, productivity and community composition (Gorham 1991; Roulet et al. 1992; Moore 2002). Increased

Abbreviations: OM, organic matter

evapotranspiration, altered precipitation, and increased frequency of extreme events (e.g., droughts) are predicted to result in a lower water table depth during the growing season (Roulet et al. 1992; Waddington et al. 1998). Impacts of the hydrological changes on ecosystem are mediated through autotrophic (vegetation) and heterotrophic (microbes) communities, and the responses of these components to changing ecohydrology may drastically change the C dynamics of peatlands, as observed during unusually warm and dry summers (Carrol and Crill 1997; Alm et al. 1999b) or after drainage for production forestry (Martikainen et al. 1993, 1995; Roulet et al. 1993, Laine et al. 1996; Minkinen et al. 1999; Hargreaves et al. 2003).

Unfortunately, there have been few studies on direct effects of climate change stressors on peatlands. Findings from related studies and generally accepted ecosystem responses to global change provide a basis to consider how forested peatlands may respond to global change stressors (Table 1), but the effects are highly uncertain. Our consideration of climate change influences on forested peatlands is based on an established foundation of ecosystem processes and effects of management regimes, especially those of peatlands drained for forestry. From that foundation, we suggest how climate change stressors may affect forested peatlands and to consider important knowledge gaps. Our framework is the basic peatland C cycle (Fig. 1), within which we consider the effects of changes in the water balance, temperature, nutrients, and plant communities. Our intent is to summarize information with respect to the processes controlling C dynamics in forested peatlands and their relationship to climate change. Our focus is northern forested peatlands, although we recognize that forested peatlands occur across a myriad of landscapes, from the boreal zone to the tropics. We have developed our discussion around a soil system, because it provides a useful framework for considering C sequestration, organic matter decomposition, plant community dynamics, and land management practices.

PEATLAND – AN ORGANIC SOIL ECOSYSTEM

Fundamentally, a peatland is a wetland ecosystem, defined on the basis of having a soil that is characterized by a relatively thick accumulation of organic matter above a mineral substrate. The definition of peatland varies by country, but it is generally considered as having at least 40 cm of organic material above the mineral substrate (Joosten and Clarke 2002). There are also other organic-matter-accumulating wetland soils having lesser amounts of surface organic matter that are subject to the same developmental influences and that provide many of the same ecological functions as peatlands. Trettin and Jurgensen (2003) recognized histic-mineral soils as having a surface organic accumulation between 5 and 30 cm. "Mire" is a term encompassing both shallow and deep accumulations of soil organic matter, broadly defined as any wetland where organic matter is accumulating on the surface regardless of depth or thickness. The organic soil layers or horizons are typically defined as having a minimum of 30% organic matter, but regional and national definitions vary from 5 to 65% (Joosten and Clarke 2002).

Organic-matter-accumulating soils are subject to the same factors of soil formation as other mineral soils: climate, topography, parent material, biota, and time (Jenny 1941). The combination of these factors has produced conditions favourable for mire development. From an ecosystem perspective, those same factors coalesce to provide the three criteria defining a wetland: hydric soils, the presence of hydrophytic vegetation, and saturated conditions during the growing season (Richardson et al. 2001). There are many different types of mires recognized around the globe on the basis of vegetation, hydrology, fertility, and peat characteristics. The development of these peatland classification systems reflects the importance of these lands for agriculture, forestry, water resources, and habitat among others; it also demonstrates the sensitivity of peatlands to a host of physical and biological influences.

THE PHYSICAL FACTORS – HYDROGEOMORPHIC SETTING

Climate, topography (e.g., geomorphic position, surface and subsurface hydrology), parent material, and time interact to affect the hydrologic regime of the site, producing an environment where hydrophytic biota predominate. Either precipitation or ground water may be the dominant source of water to the peatland (Verry 1997; Richardson et al. 2001). Understanding the contributing sources of water and the inherent variation in the water balance of the peatland is fundamental to considering the potential effects of climate change. The effect of land use or restoration practices on the water balance must also be considered in managed peatlands.

There are two hydrologic regimes used to characterize the hydrology of the peatland (Ingram 1983). Bogs are peatlands whose hydrologic regime is determined almost entirely through the precipitation cycle and evapotranspiration. In contrast, a fen is a peatland whose hydrologic regime is mediated primarily by ground water processes. These two basic hydrologic regimes have inherent differences in nutrient content; hence the development of terms to reflect a combination of hydrologic drivers and fertility (Moore and Bellamy 1974). Soil saturation is the prerequisite for the development of anaerobic conditions. The degree of saturation in combination with the parent material, accumulated organic matter, and vegetation affect the anoxic conditions and the corresponding reduction reactions (Vepraskas and Faulkner 2001).

BIOTA – PLANT-MEDIATED C SEQUESTRATION

Hydrology, in combination with the plant community, regulates the development of the peatland and dynamics of the C cycle. That development process may include a wide variety of successional pathways, including aquatic, non-forest and forest vegetative communities, as well as development of upland sites through paludification or the filling of aquatic sites through terrestrialization (Paavilainen and Päiväne 1995). The common denominator is soil saturation, which is the principal factor affecting the development of peat soil. Forested peatlands typically develop on sites that have slightly deeper and fluctuating water table during the grow

Table 1. Effect of global climate change factors on organic matter production (NPP) and decomposition in forested peatlands.²

Factor	NPP	Decomposition	Comment
+ temperature	+/- (growing season, + (activity) respiration)		Warmer temperatures may extend growing season, but also increase respiration losses. Microbial activity generally increases with temperature
+ precipitation	+/- (avail water)	- (anoxia)	Where water is limiting, increased precipitation may increase productivity. Conversely, increased precipitation on peat soils may cause extended periods of anoxia reducing both production and decomposition
+ N deposition	+ (nutrient)	+ (nutrient)	N is a common limiting element, hence deposition is expected to increase productivity and decomposition
+ atmospheric CO ₂	+ (efficiency)	+ (BG input)	Elevated CO ₂ increases photosynthetic efficiency; hence OM inputs may increase, causing a corresponding increase in heterotrophic activity
+ atmospheric ozone	- (stress)	- (OM input)	Ozone has a toxic effect on plants, hence productivity is expected to decline. No studies on peatland vegetation

²The sign indicates either a positive or negative influence, the primary cause indicated parenthetically. References and rationale are discussed in the text.

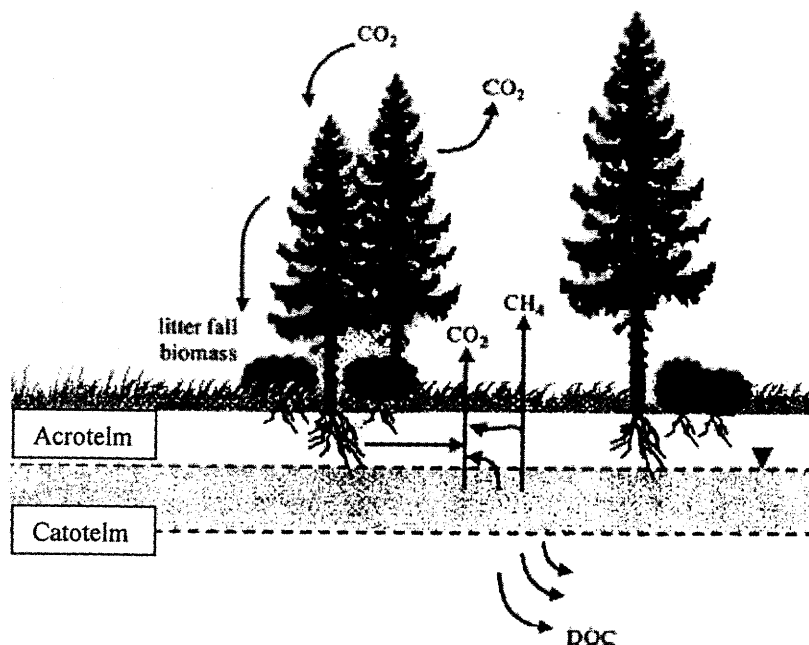


Fig. 1. Peatland carbon cycle (from Trettin and Jurgensen 2003). Fixation occurs through photosynthesis in the tree, shrub and ground layers; organic matter inputs to the soil via above- and below-ground litter; losses via heterotrophic and autotrophic respiration, and leaching. The water table (V) controls the volume of aerated soil.

ing season (Westman et al. 1985), or soil water that contains free oxygen necessary for tree root functioning.

Organic matter, derived from either above-ground or below-ground biomass production, is the principal source of soil C. Productivity among wetland forest types varies widely reflecting differences in climate, hydrology, and vegetation community. The effects of climate are evident with productivity generally being higher in the temperate forests, as compared with the boreal forests (Trettin and Jurgensen 2003); however, there is considerable variability among wetland types within a climatic zone. The composition and physiognomy of the peatland vegetation are to a large extent regulated by water table level and soil fertility. Peatland productivity ranges between 300 and 1000 g m⁻² yr⁻¹ (Reader and Stewart 1972;

Grigal et al. 1982; Trettin and Jurgensen 2003), with the understory vegetation (i.e., bryophytes, sedges, shrubs) typically comprising a significant proportion of the net C sequestration (Reinikainen et al. 1984; Grigal 1985). It is likely that the reported estimates of peatland productivity are low because of the paucity of measurements on below-ground sequestration (Trettin and Jurgensen 2003). Correspondingly, there is considerable uncertainty about the relative contributions of above- and below-ground biomass to the soil organic matter pool in peatlands. Understanding the production dynamics is important because there is a direct relationship between net ecosystem productivity and greenhouse gas (CO₂ and CH₄) emissions in undisturbed peatlands (Bubier and Moore 1994).

The type of peat and the organic matter (OM) accumulation rate are determined by the type of vegetative community and rates of OM productivity and decay, which in turn are regulated by the depth and duration of the water table relative to the soil surface. A persistent lowering of the water table level and the consequently improved growth conditions for arboreal plants will initiate a secondary succession, which, with the exception of the most nutrient-poor sites, will lead to a decrease in the abundance and biomass of species adapted to wet conditions, such as many sedges and herbs, and the proliferation of shrubs and trees (Laine et al. 1995a; Laiho et al. 2003). Mosses may retain their functional importance after adaptation at the community level (Laiho et al. 2003). However, *Sphagnum* mosses are sensitive to water table depth (Gignac et al. 2000), and a persistent lowering of the water table may result in their demise from the site (Mulligan and Gignac 2001). The change in the growth form dominance in favour of arboreal plants has a major influence on total plant biomass, even though total net primary production may not change as dramatically (Reinikainen et al. 1984; Saarinen 1996; Finér and Laine 1998). For instance, in the pristine oligotrophic fen sites studied by Laiho et al. (2003), the total (above- and below-ground) plant biomass was approximately 1700 g m^{-2} , two-thirds of which was found in the understory vegetation (predominantly mosses and graminoids). Within 50 yr following water-level drawdown induced by ditching, the total biomass had increased sevenfold and more than 90% of it was tree biomass (Fig. 2A).

Changes in the vegetation composition are clearly reflected in the litterfall composition. Continuing with the previous example, on undrained sites, approximately 80% of the annual above-ground litterfall was estimated to be derived from mosses and sedges (Fig. 2B). Below-ground, an estimated 80% of the litter was derived from sedges. Within 20 yr after water-level drawdown, shrubs and trees had become the major litter source, producing 90% of the total vascular plant litter and 75% of the total litter estimate, including moss litter. Over time, the composition of litterfall from arboreal plants changed gradually as a result of increased proportions of woody debris and cones (Fig. 2C). This kind of change will partly counteract the enhancing effect of water-level drawdown on decomposition processes. Graminoid and herbaceous litters, which are the major vascular plant litter types in many minerotrophic peatland types, decompose faster than foliage litter from shrubs and trees (Hobbie 1996; Szumigalski and Bayley 1996), which may become the major litter types after water-level drawdown. Woody materials, branches and cones, decompose especially slowly (Taylor et al. 1991; Hobbie 1996). Both *Sphagnum* mosses and forest species that increase after water-level drawdown, such as *Pleurozium screberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G., generally decompose slowly as well (Hobbie 1996; Karsisto et al. 1996). Forest succession, with higher moss and woody litter input, lower soil temperature (Minkinen et al. 1999) and higher acidity of the surface soil (Laine et al. 1995a, b) may lead to higher amounts of soil OM (Vompersky et al. 1992;

CARBON CYCLING PROCESSES IN PEATLAND FORESTS – CLIMATE CHANGE EFFECTS

Primary Production

There are very few studies addressing the direct effects of climate change (i.e., elevated CO_2) on peatland plant species' productivity or photosynthesis; accordingly, we assume that they will respond similarly to other vascular plants. With respect to non-vascular plants, Jauhiainen and Silvola (1999) reported an increase in the photosynthetic rate of *Sphagnum fuscum* under elevated CO_2 conditions. A change in precipitation regime that results in a lower water table level during the growing season is a climate change effect that can be characterized through existing drainage study sites. In addition to the change in plant community described above, there is typically a commensurate increase in the productivity of the tree species (Paavilainen and Päivänen 1995). The growth response is attributed to an increase in aerated soil volume during the growing season. Presumably there are also changes in above- and below-ground allocation, but those effects need to be measured.

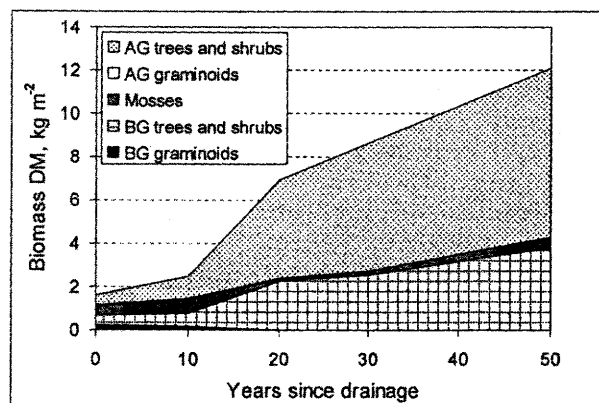
Heterotrophic Decomposition of Organic Matter in Peat Soils

Peatlands are C-accumulating ecosystems with the average long-term C accumulation rates varying between 2 and $89 \text{ g m}^{-2} \text{ yr}^{-1}$ depending on latitude and wetland type (Korhola et al. 1995; Tolonen and Turunen 1996; Bridgman et al. 2001); in the boreal zone the long-term rate is usually within 13 to $18 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Tolonen and Turunen 1996; Clymo et al. 1998). Soil OM decomposition is regulated by temperature, moisture, aeration, organic matter quality, pH, and available nutrients. Unfortunately, too few studies have considered the interactions of these factors under anoxic conditions that are typical of peatlands (Eijsackers and Zehnder 1990); however, single-factor studies among different peatland types provide insight on how climate change stressors may affect OM decomposition.

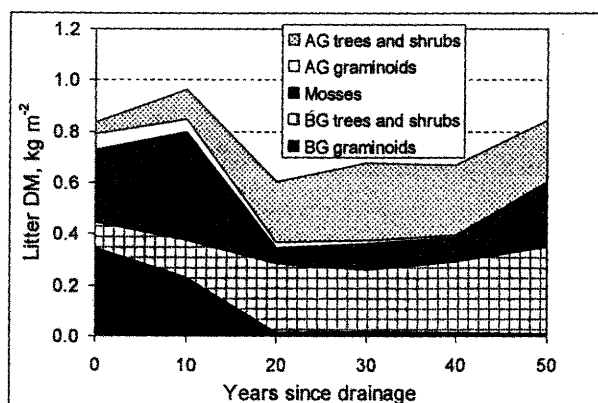
Water content is the principal factor controlling OM decomposition in peatland soils, principally through its affect on soil aeration content. When the soil is saturated, oxygen supply will be regulated by slow diffusivity, microbial and root activity and inputs from ground water. Typically, anoxic conditions ensue following 3–5 d of water saturation (Mausbach and Richardson 1994). Under anoxic conditions in peatlands, phenols, from the detritus accumulate in the soil, thereby effectively reducing the rate of OM decomposition by inhibiting microbial activity (Freeman et al. 2001).

Most peat soils are not saturated continuously to the surface; fluctuating water tables and precipitation patterns induce varied periods of wetting and drying within a zone, called the acrotelm (Belyea and Clymo 2001). Underlying the acrotelm is the permanently saturated peat, or catotelm. The acrotelm in fens is much thinner than in bogs because they are sustained primarily by ground water discharge. In contrast, bogs have a thicker acrotelm due to the dependence of the water table position on precipitation and evapotranspiration. The micro-topography in peat soils also influences soil aeration, with feedbacks to organic matter

A



B



C

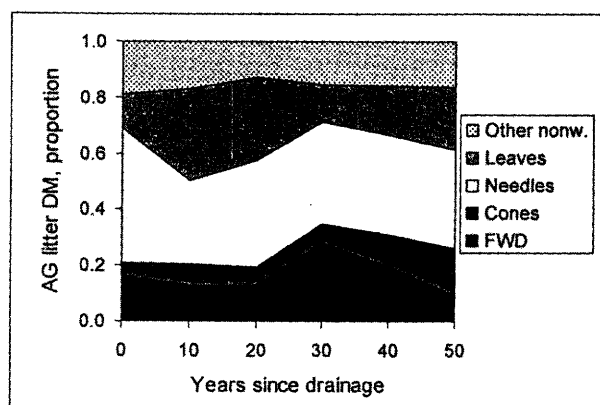


Fig. 2. Evolution of (A) total plant biomass, (B) annual litterfall, and (C) composition of arboreal litter [above-ground (AG)], following water-level drawdown in oligotrophic sedge-pine fens. Based on the chronosequence study by Laiho et al. (2003) where the waterlevel draw-down was induced by forestry drainage. DM = dry mass (matter) (105°C), FWD = fine woody debris, BG = below-ground.

decomposition rates and plant community composition (Farrish and Grigal 1988; Hogg 1993; Hogg et al. 1992). Typically, hummocks have longer periods of aeration than hollows.

Since microbial activity is strongly regulated by temperature (Savage and Davidson 2001, Fierer et al. 2003), temperature is a principal factor regulating OM decomposition in aerated zones within the acrotelm (Bridgham et al. 1991;

Hogg et al. 1992; Trettin et al. 1996). There is an interaction among soil temperature and water table depth (Silvola et al. 1996; Hökkä et al. 1997), and under saturated conditions the temperature response may be dampened as a result of a low supply of oxygen and phenol inhibition (Freeman et al. 2001).

The temperature in peat soils corresponds to the air temperature and exposure to sunlight; accordingly, changes in community composition and canopy structure are factors that may affect soil temperature. The water content of the soil is also an important factor regulating soil temperature (Lähde 1969). For example, long-term changes in peatland vegetation following drainage may actually lower soil temperatures compared with the pre-drainage condition (Minkinen et al. 1999) as a result of shading and more aerated surface soils.

The quality or structural composition of soil organic matter is another factor affecting the rate of OM decomposition (Howard-Williams et al. 1988). Organic matter quality is determined by organic chemical content and structure, which is a function of plant species, soil properties in which the plants were growing, and the length of time and conditions under which it has been exposed to decay (Wieder and Yavitt 1991). Despite the varying influences on OM decay, which in turn cause the decomposition rates to vary among peatlands in the short term, over the long-term, decomposition rates typically converge after 15–20 yr, exhibiting an asymptotic rather than exponential form (Latter et al. 1998).

Mechanistically, whether a peatland will remain a C sink, become a stronger sink, or become a source of C to the atmosphere following water level drawdown will depend on the rate of decomposition of the "old", pre-water-level-drawdown peat, and the rates of inputs and decomposition of the "new" organic matter entering the system as litter produced under the new environmental conditions. Further, the effects of water-level drawdown on OM decomposition rates may not always be straightforward or consistent. Among the relatively few field studies on drainage-induced changes in OM decomposition rates, increase, decrease, and no change have all been observed (Liefers 1988; Minkinen et al. 1999; Domisch 2000; Laiho et al. 2004). Accordingly, it is difficult to draw consistent conclusions from these studies, and it is overly simplistic to consider the affects of regulating factors individually. For example, the presumption is that OM decomposition will be increased in drained peatlands. However, OM decay rates may actually be reduced in the surface layers as a result of dry conditions (Liefers 1988; Laiho et al. 2004), lower soil temperature (Minkinen et al. 1999), or higher acidity (Laine et al. 1995b; Minkinen et al. 1999).

Greenhouse Gas Fluxes and the Carbon Balance in Peatlands

Carbon Dioxide Soil Efflux

Carbon dioxide efflux from the peat surface represents the combined influences of heterotrophic (e.g., microfauna) and autotrophic (e.g., plants) respiration. It is commonly used as a metric of change in the soil C cycle in response to a stress factor or perturbation regime. With respect to climate change, while temperature is frequently the focus of consid-

eration, the indirect impacts of a warming climate may have more significant changes on soil C dynamics (Gorham 1991). Higher air temperatures increase evapotranspiration and lower the humidity, which may result in the lowering of the water table by 14–22 cm in boreal peatlands (Roulet 1991). Water level drawdown increases the aerobic volume in surface peat and leads to increased CO₂ emissions through enhanced aerobic OM decomposition (Silvola 1986; Moore and Dalva 1993; Silvola et al. 1996); however, the relationship of water table position with CO₂ efflux from the peat surface is highly variable (Fig. 3). For any given water table depth, the observed range in CO₂ efflux varied 200–500%, across a wide variety of peatland types.

The increase in soil respiration following water level drawdown after artificial drainage has often been regarded as an indicator of C loss from the accumulated peat (e.g., Silvola 1986; Gorham 1991; Nykänen et al. 1997). In peatlands drained for forestry, net primary production, biomass, litterfall, and autotrophic respiration increase after water level drawdown (Laiho et al. 2003). It has been estimated that roots (Silvola et al. 1992) and new litter (Minkinen et al. 2004) together may comprise two-thirds of the measured CO₂ efflux (i.e., soil respiration) in peatlands with established drainage systems. Thus, an increase in soil respiration does not necessarily lead to a decrease in the peat C pool. Changes in primary productivity and carbon storage of the peat-forming vegetation, including trees, are equally important in understanding the effects of water level drawdown (Gorham 1991; Hogg et al. 1992). Direct measurements of changes in peat C pool following water table drawdown are rare, probably because of methodological difficulties, but both decreases (Braekke and Finér 1991; Sakovets and Germanova 1992; Gustafsson 2001) and increases (Minkinen and Laine 1998a; Minkinen et al. 1999) have been reported. As C stores in vegetation nearly always increase following forestry drainage (Laiho et al. 2003), peatlands may remain C sinks in drier climate despite possible C losses from the peat due to increased rates of OM decomposition (Minkinen et al. 2002; Hargreaves et al. 2003).

Methane Soil Efflux

Methane (CH₄) is formed by methanogenic *Archaea* in anaerobic conditions and is oxidized into CO₂ in aerobic conditions by methanotrophic bacteria. Most of the CH₄ emitted from undisturbed peatlands originates from fresh organic matter deposited directly into the anoxic peat layers by deep-rooted sedges (Whiting and Chanton 1993; Bubier 1995; Mikkilä et al. 1995; Ström et al. 2003). Since CH₄ production and oxidation are sensitive to micro-sites and soil aeration, water level changes associated with an altered hydrologic regime will change CH₄ dynamics in the peatland (Bubier et al. 1995a; Saarino et al. 1997). Following drainage for forestry, the most distinctive change in CH₄ dynamics takes place when sedges are replaced by vegetation adapted to drier conditions, and direct C deposition into the catotelm is diminished. The predicted water level drawdown following climate change is smaller than that after forestry drainage, but there is evidence that even a small

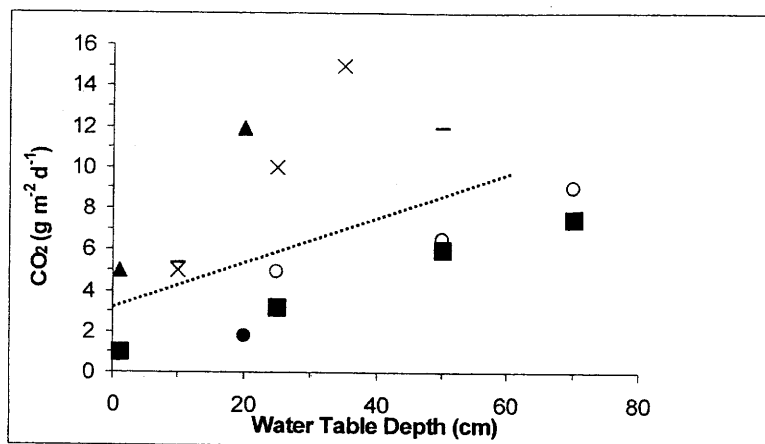


Fig. 3. Carbon dioxide efflux from peatland surfaces versus water table depth. Each symbol represents field measurements except Freeman et al. (1993), which was a laboratory study. The linear regression is shown as a dashed line ($y = 0.11x + 3.21$; $R^2 = 0.33$). Data sources: O, Moore and Knowles (1990) (fen); ■, Moore and Knowles (1990) (swamp), ▲, Bubier et al. (1998); —, Silvola et al. (1996); ×, Kim and Verma (1992); ●, Freeman et al. (1993).

change in water table may induce a similar hydrosereal succession from sedge communities to hummock communities (Bubier et al. 2003). Strack et al. (2004) also found significant reductions in CH_4 emissions following water table drawdown in a fen, but they noted that hollow micro-site positions could still be strong sources of CH_4 , especially when vegetative productivity was stimulated by the altered hydrology.

A water table depth of 10–20 cm below the peat surface appears to be a critical threshold for CH_4 emissions from northern peatlands. When the water table is below that depth, CH_4 emissions from the soil surface are reduced to near-zero (Fig. 4). In Finnish peatlands, CH_4 emissions have markedly decreased (from 3–30 on the undrained sites to -5 – $6 \text{ g C m}^{-2} \text{ yr}^{-1}$ on the drained sites) following water level drawdown (Nykänen et al. 1998). The decrease is lowest in ombrotrophic pine bogs and greatest in meso-oligotrophic sedge fens, which undergo the greatest change in vegetation and physico-chemical environment (Minkinen et al. 1999) and often act as net sinks for atmospheric CH_4 after water level drawdown (Lien et al. 1992; Glenn et al. 1993; Martikainen et al. 1995; Nykänen et al. 1998). There is a positive relationship between peat temperature and CH_4 flux from the peat surface (Bellisario et al. 1999), although the observed range in flux is large for any given temperature (Fig. 5). There is a distinct interaction between peat temperature, water table position, and peatland micro-site (e.g., hummock vs. hollow) on CH_4 efflux, with the hollow position exhibiting higher fluxes (Macdonald et al. 1998). It is important to note that CH_4 fluxes from peatlands are not confined to the growing season or snow-free period; winter flux in a northern peatland has been measured to be approximately 10–25% of the annual flux (Alm et al. 1999a) and 2–9% of the annual flux in a temperate peatland (Melloh and Crill 1996). Elevated atmospheric CO_2 concentrations have been shown to increase CH_4 flux in an oligotrophic peatland (Saarnio et al. 1999), presumably in response to increased productivity (Bellisario et al. 1999).

PERSPECTIVES ON THE EFFECTS OF GLOBAL CHANGE ON FORESTED PEATLAND C DYNAMICS

In an undisturbed state, peatlands are not an invariant sink for C. Instead, the annual C balance in natural peatlands is sensitive to minor changes in climatic conditions that alter the hydrologic regime (Alm et al. 1999b). In the short-term, peatlands can be expected to be either sources or sinks for C; however, over the long-term, hydrologic conditions must be sufficiently stable to sustain a vegetation community that sequesters C, and a soil environment that is sufficiently low in oxygen to constrain OM decomposition rates.

Peatland management (e.g., silviculture, restoration) is another factor that must also be considered with the natural variation and uncertainties associated with climate change (Trettin and Jurgensen 2003). Forest harvesting influences the peatland water balance by reducing evapotranspiration, which may result in a higher water table for a period of years. Correspondingly, the soil temperature regime may increase as a result of increased insolation, thereby enhancing C turnover. Restoration of drained peatlands may actually increase CH_4 emissions as a result of longer hydroperiods near the soil surface (Komulainen et al. 1998); that effect may offset gains in C sequestration when considered on a radiative forcing basis.

Wildfire is another significant factor that can reduce the size of the peat soil C pool. Some climate change scenarios suggest more frequent and intense wildfires in the boreal zone resulting in significant losses of soil C (Turetsky et al. 2002). While susceptibility of a peatland soil to wildfire is largely dependent on the water table position, a nominal consumption of 20 cm of peat would be the equivalent of approximately 280 yr of C accumulation (basis: bulk density = 0.09 g cm^{-3} , C content = 50% OM, C accumulation rate = $32 \text{ g m}^{-2} \text{ yr}^{-1}$). In addition to the loss from direct combustion, fire will also alter the C balance of the peatland through changes in productivity and species composition.

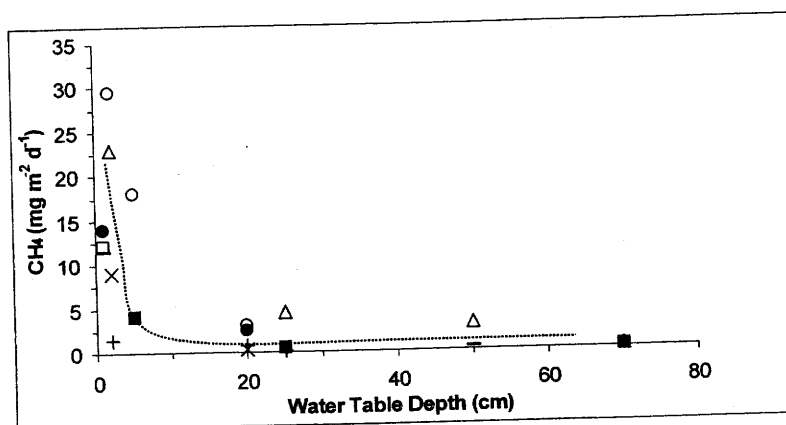


Fig. 4. Methane efflux from peatland surfaces versus water table depth. The log-transformed trend line is shown ($y = -3.86\ln(x) + 15.44$; $R^2 = 0.50$). Each symbol represents field measurements except Freeman et al. (1993), which was a laboratory study. Data sources: Δ , Moore and Knowles (1990) (fen); \blacksquare , Moore and Knowles (1990) (swamp); \bullet , Freeman et al. (1993); \times , Alm et al. (1999a); $+$, Bubier and Moore (1994); \circ , Macdonald et al. (1998); $+$, Bubier et al. (1995b); \square , Bellisario et al. (1999).

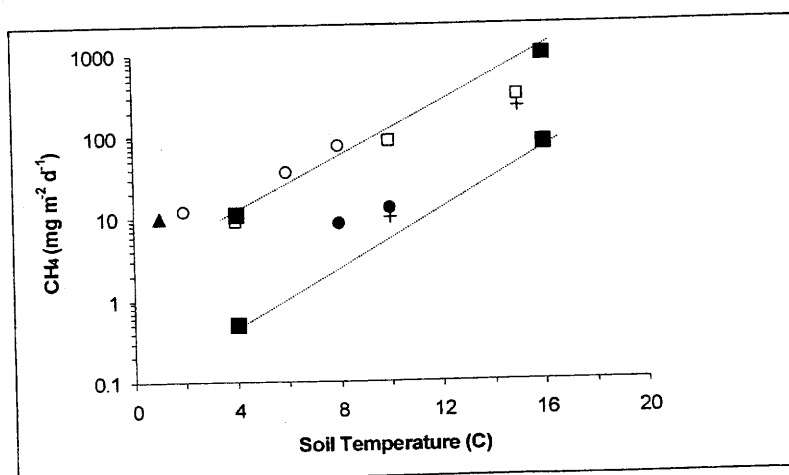


Fig. 5. Range in observed methane efflux from peat surfaces versus soil temperature. The dashed lines bound the range in observations summarized by Bartlett and Harris (1993). Data sources: \blacksquare , Bartlett and Harris (1993); $+$, Wilson et al. (1989); \blacktriangle , Dise et al. (1992); \circ , Alm et al. (1999a); \square , Bubier and Moore (1994); \bullet , Fowler et al. (1995).

Unfortunately, there is very little information addressing the peatland response to wildfire:

The intricacies of the C cycle in peatlands need further study, especially with respect to (1) the microbial ecology and biochemistry regulating OM turnover, and (2) the interaction among hydrology, organic matter quality, temperature, and soil nitrogen on above- and below-ground C sequestration and OM decomposition. Understanding how these processes are affected by restoration and wildfire are particularly important research needs. The paucity of process-based soil C models that are applicable to peatlands (Trettin et al. 2001) is a serious limitation to assessing climate change impacts. Recent developments of Wetland-DNDC (Zhang et al. 2002; Li et al. 2004), PCAR (Frolking et al. 2001) and WMEM (Cao et al. 1996), for example, are

soils and biogeographic zones is needed, as well as careful attention to the complexities of scaling for regional assessments.

Long-term experiments are fundamental to addressing basic information needs and providing a basis for model applications. Most of the information on peatland processes is developed through short-term (e.g., 3–5 yr) studies. This timeframe is too short to incorporate the inherent variability in ecosystem processes, especially when the effects of management or climate change are incorporated. Latter et al. (1998) demonstrated that short-term differences in OM decomposition have little bearing on the net effect. Accordingly, without models, it is exceedingly difficult to interpret the short-term observations with respect to climate change stressors, which are typically manifest over decades. The value of long-term observations and study are demon-

strated by the Finnish peatland response studies (Minkkinen and Laine 1998; Minkkinen et al. 2004), where the cumulative, long-term response would not align with effects predicted based on short-term assessments. Maintaining selected long-term study sites is critical to confirming the C dynamics in experimental peatlands.

The most effective approach for considering the effects of climate change on peatland C dynamics is through the basic soil development model [peat soil = f (climate, biota, time, topography, and parent material)]. This framework ensures that each of the principal components affecting the C cycle is considered. Interactions between changes in the water budget and biota will cause major effects to the peatland C cycle, because the degree and extent of saturated soil conditions is such a strong determinate of plant community composition and productivity, and the soil fauna, and microbial activities. An integrated assessment of a lower mean water table level scenario on northern peatlands (Laine et al. 1996) would be a worthwhile exercise for other scenarios and to integrate them at the landscape scale. Other stressors, such as nitrogen deposition, increased atmospheric ozone, and acid deposition, will also influence the peatland C cycle, but the effects will have to be considered through the hydrologic cycle.

CONCLUSIONS

Peatlands are a significant C reservoir, comprising the largest single soil pool. Accordingly, understanding how global change, including land management, will affect the C balance is fundamental to all large-scale assessments of the terrestrial C cycle and the associated linkages to climatic warming and radiative forcing (e.g., Roulet 2000; McLaughlin 2004). Since direct studies of climate change "stressors" in forested peatlands have not been done, we have used the foundation provided by soil science, peatland ecology, and management research to consider how peatlands may respond under a changed climate. On the basis of those studies, we conclude that climate change influences on northern peatlands will be mediated primarily through changes in the hydrologic cycle. Only in the arctic, where permafrost is lost due to climatic warming, is temperature expected to be the dominant factor affecting the peatland C balance.

The widely varying predictions about future climate conditions in northern latitudes makes it very difficult to forecast specific impacts on the peatland C balance. Changes in precipitation patterns and quantities and temperature will affect C turnover in peatlands, but the C balance will be mediated through interactions among vegetation, microorganisms, and abiotic conditions (e.g., soil temperature, aeration, and water, nutrient availability). With the aforementioned caveat, we are comfortable concluding that a changed peatland water balance resulting in a lower water table will decrease soil CH₄ emissions and increase CO₂ emissions; however, the increase in CO₂ emissions does not necessarily imply a decrease in the peat C pool. In the long term, lower water tables may increase CO₂ sequestration to the ecosystem because of increased plant productivity and vegetation succession (Vompersky et al. 1992; Minkkinen and Laine 1998). The reduction in CH₄ flux with lower water tables is also a significant factor reduc-

ing the global warming potential of emissions from northern peatlands (Laine et al. 1996). One consequence of enhanced peatland productivity, whether from altered hydrology or elevated CO₂, may be an increase in dissolved C export from the site (Freeman et al. 2004).

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